CHARACTERISTICS OF THE BAT (CHIROPTERA) POPULATION IN PROTECTED AREAS IN THE NORTHERN AND MIDDLE TAIGA SUBZONES OF EUROPEAN RUSSIA

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Received: 16.04.2020. Revised: 12.10.2020. Accepted: 22.10.2020.

The overall bat (Chiroptera) fauna of Protected Areas in the forest zone of European Russia has not yet been assessed, although papers on some Protected Areas are being published quite regularly. Along its north-to-south gradient, this extensive area spans a great variety of habitats suitable for bat populations with vastly diverse compositions. In our review of bat species, we focused on eight Protected Areas in the northern and middle taiga, as well as on a comparative summary of the faunal data for the forest zone of European Russia in general. Surveys using a bat detector and by mist-netting resulted in identification of the species composition, relative abundance, relative density and spatial distribution of bats in Protected Areas. The following nine bat species were recorded: *Myotis nattereri, M. mystacinus, M. brandtii, M. daubentonii, M. dasycneme, Plecotus auritus, Nyctalus noctula, Eptesicus nilssonii, Vespertilio murinus*. We regularly recorded ultrasonic signals from *Plecotus auritus, Nyctalus noctula* and *Vespertilio murinus* up to 66° N, which is much farther north that the species ranges indicated on IUCN maps. This result came as a surprise, considering there had been no specialised censuses in the Republic of Karelia or the Arkhangelsk region for decades. In Protected Areas, bat communities were dominated by *Eptesicus nilssonii*, which is specific to the northern taiga and middle taiga subzones. We discuss some ecological preferences of this species, such as a relatively higher tolerance of *E. nilssonii* towards temperature, but not towards air humidity in winter roosts, which may help it to thrive at high latitudes. At the same time, *E. nilssonii* is either missing from more southern parts of the forest zone or its relative abundance there is lower, while the dominant faunal elements are *Myotis daubentonii* (Darwin State Nature Reserve), *Nyctalus noctula* (Smolenskoye Poozerye National Park, Oksky State Nature Reserve, Bryansky Les State Nature Reserve) and *Pipistrellus nathusii* (Prioksko-Terrasny State Nature Reserve). Additionally, bat captures by using mist nets in the Vodlozersky National Park revealed the northernmost records of *Myotis mystacinus* in European Russia (62.224867° N, 37.081629° E and 62.466342° N, 36.673240° E). Finally, we argue that recent bat records demand a revision of the status of bats in regional Red Data Books.

Key words: distribution, Red Data Book, relative abundance, relative density, species composition

Introduction

In contrast to the majority of West European countries, European Russia spans a wide spectrum of vegetation zones from north to south, the forest zone being the most extensive one. All of this area, from the northern taiga in the Kola Peninsula to nemoral forests of Central Russia, is highly attractive for bats (*Strelkov & Ilyin*, 1990). The latitudinal sequence of vegetation zones offers a variety of quite specific habitats for bats. Owing to the availability of shelter, foraging and breeding environments these territories can be utilised by both migratory and sedentary bat species. There is zonation in the microclimates of underground shelters and their usability for individual bat species in relation to the different energy costs of hibernation (Anufriev, 2008). The bat species diversity is known to be closely correlated with latitude, climatic features, duration of seasons (Ulrich et al., 2007; Michaelsen et al., 2011), altitudinal and temperature gradients (Michaelsen, 2016). The European bat fauna gets poorer from the south to the north of the continent, so that eventually only the northern bats live and breed above the Arctic Circle (Rydell et al., 1994). It enjoys some advantages over other species, including physiological-biochemical parameters, high resistance to negative temperatures, and a high ecological valence at hibernacula (Belkin et al., 2019a).

Climate change and urbanisation are the two leading processes that can drive the range expansion of bats (Hamphries et al., 2002; *Strelkov*, 2004; Rebelo et al., 2010; Ancillotto et al., 2016) and insects, i.e. their potential prey (Shutova, 2016), in the forest zone, too. A wide application of acoustic observations in ecological and biogeographic studies, in particular at the northern limits of species ranges (Ahlén et al., 2007, 2009; Jones et al., 2013; Poerink et al., 2013; Rydell et al., 2014, 2020; Michaelsen, 2016; Belkin et al.,

2018, 2019b; Tidenberg et al., 2019), helps quickly detect the dynamical processes in the species composition, abundance, migratory behaviour and distribution of certain bat species.

The key challenges in the study and conservation of chiropterans in Russia, including Protected Areas (PAs), have been articulated by a number of specialists (Snitko, 2000; Bolshakov et al., 2005; Vekhnik & Sachkov, 2005). But many of them still remain to be addressed. Owing to the high interest in bats, observed foremost in PAs, chiropteran checklists have been compiled for many PAs, patterns of their stay and distribution across the areas were determined, the ecological characteristics of species were better studied, etc. However, previous fieldwork was mostly done in the summer seasons, when both sedentary and migratory bats can be encountered. The vast dataset from study years has been chiefly published in Russia. But for a variety of reasons, unfortunately, it did not represent the status reports of European chiropterans or papers on the biogeography of this group of animals on the continent (Mitchell-Jones et al., 1999; Pereswiet-Soltan, 2007; Dietz et al., 2011).

Russia's well-developed Protected Area network (in many of which bats have been studied) permits defining the aim of this paper, which concerns the investigation of spatial patterns in the characteristics of chiropteran communities in the forest zone of European Russia. The tasks include a brief analysis of the latitudinal changes of the species composition across the forest zone and first conclusions on the bat fauna in PAs of the least studied region, the northern and middle taiga subzones (Bogdarina & Strelkov, 2003).

Material and Methods

The geographical patterns in the distribution of chiropteran communities in PAs in the forest zone (Fig. 1) were analysed based on recent literature and the results of our own fieldwork in the Republic of Karelia, Murmansk region and Arkhangelsk region in late July – August of 2016–2019. Fieldwork was carried out in state nature reserves (SNR), national parks (NP) and other Pas, namely natural parks, nature sanctuaries, and natural monuments. Their status is defined according to the Russian Federal Act on Protected Areas №33-FZ (dated by 14.03.1995). We conducted car surveys in summer using a static bat detector in eight PAs. The total length of car routes surveyed was 1040 km, of which 600 km were in fifteen 40-km transects. In the PAs with a poor road network, surveys were conducted on foot with sampling at fixed points, like bridges, shores and banks, forest glades, isolated buildings, and others. Water bodies in the PAs were surveyed along 120 km of transects from motor boats, i.e. nine water transects, 12 km to 20 km each depending on the size of the water body. Visual observations with identification were based on exterior traits and flight characteristics were used. Two dead bats collected during fieldwork were treated. Counts at fixed points lasted 278 h.

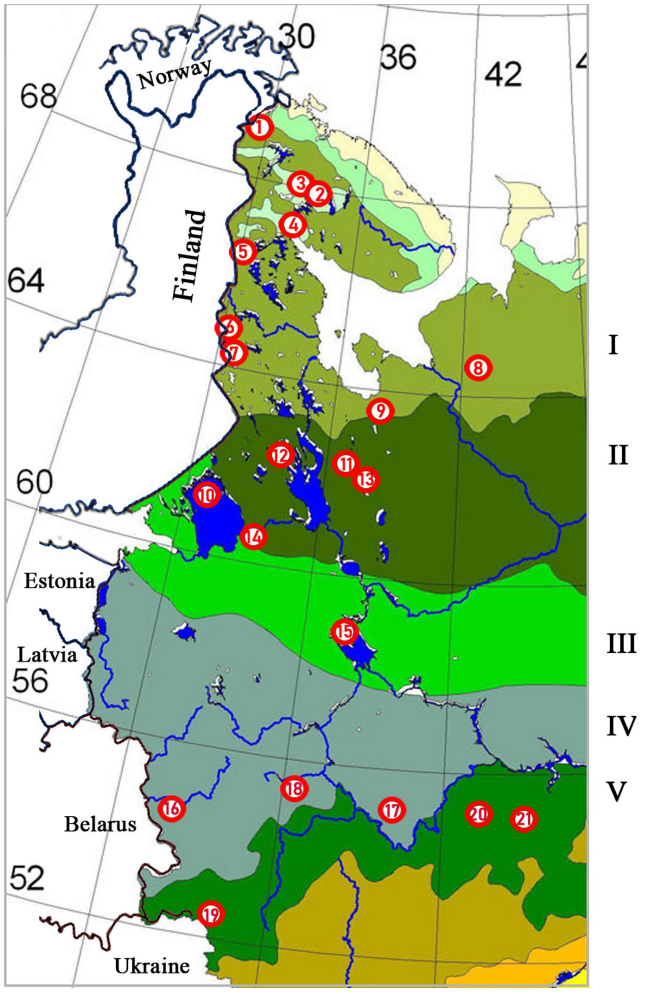

Fig. 1. Locations of the studied Protected Areas in the forest zone of European Russia. Designations: I – northern taiga subzone (1 – Pasvik State Nature Reserve, 2 – Avrorin Polar-Alpine Botanical Garden Institute, 3 – Laplandsky State Nature Reserve, 4 – Kandalakshsky State Nature Reserve, 5 – Paanajarvi National Park, 6 – Kalevalsky National Park, 7 – Kostomuksha State Nature Reserve, 8 – Pinega State Nature Reserve, 9 – Kozhozersky Regional Landscape Reserve), II – middle taiga subzone (10 – Valaam Archipelago Regional Nature Park, 11 – Vodlozersky National Park, 12 – Kivach State Nature Reserve, 13 – Kenozersky National Park, 14 – Nizhne-Svirsky State Nature Reserve), III – southern taiga subzone (15 – Darwin State Nature Reserve), IV – subzone of subboreal forests (16 – Smolenskoye Poozerye National Park, 17 – Oksky State Nature Reserve, 18 – Prioksko-Terrasny State Nature Reserve), V – subzone of nemoral forests (19 – Bryansky Les State Nature Reserve, 20 – Mordovia State Nature Reserve, 21 – Smolny National Park) (Map with modifications according to Zaugolnova & Martynenko, 2014).

Summer counts of bats covered an area from 61° N, 29° E to 66° N, 44° E. The species diversity, distribution and relative abundance (%) were determined along routes surveyed by car driven at around 40 km/h throughout the night. Bat counts at fixed points were run in the automatic mode throughout night time, with the detector deployed 1 h before sunset and collected 2 h after sunrise. Each night a car route started with surveying a 40-km transect and then continued until sunrise. Counts commenced 45 min after sunset (Russ et al., 2003; Jones et al., 2013) to enable determination of the relative density of bats (individuals per 1 km) in 40-km transects, in addition to the indices listed above. The counting surveys employed a static detector Song Meter SM2 Bat+ (USA) with omnidirectional external microphone installed on top of the car roof. Detector-facilitated bat counts at water bodies were carried out from motor boat driven at 10–15 km/h along the shoreline at 20–30 m distance.

Species identification was done automatically by Kaleidoscope Pro software (ver. 3.1.1.). We used the classifier for Finland so that the software does not need to run through the entire European list of bat when processing the records. This, given the low bat diversity in our region, significantly improved the accuracy of species identification, which many specialists now believe to be insufficiently reliable and credible (Russo & Voigt, 2016; Rydell et al., 2017). *Myotis brandtii* Eversmann, 1845 and *M. mystacinus* Kuhl, 1817 were not differentiated since the characteristics of the signals they emit were identical. The software allows identifying a species uniquely at a known confidence level using a series of three to several tens of signals. In faunal studies, this can be regarded as a positive sign, indicating the presence of a species in the area. Specification of the real time of recording for echo-location files makes it easier to spot individual bats along the route. The time interval between files was usually 1 min to 60 min. Given the speed at which the car was moving (10–11 m/s), all signals of one species received within less than 10 s were deemed to belong to one individual. This approach minimises the interference of a sole bat flying around the detector with the output (Miller, 2001).

In PAs, sampling was mostly performed by a non-contact method (ultrasound detection), with only one occasion of bat capturing by mist nets in combination with recording by a detector. This approach is particularly relevant for PAs, and enables not only covering specific key sites in the PAs (Vekhnik & Sachkov, 2005; Shpak, 2019), but also taking a census of bats throughout the available area at a minimum cost.

Netting of bats (with two 3 × 6 m mist nets with 15 mm mesh size) was carried out in Vodlozersky NP during seven nights. The animal species, sex and time of capture were recorded, after which they were placed in a canvas bag to be released early in the morning. *Myotis brandtii* and *Myotis mystacinus* were determined morphologically (Hanák, 1970; Baagøe, 1973; Strelkov & Buntova, 1982; Lehmann, 1983–1984) based on penis shape in males and cranial material (bat bagging permit №00015 from the Republic of Karelia Ministry of Natural Resources and the Environment). We also controlled four potential bat day-roosts. *Pipistrellus* records from PAs in sub-boreal and nemoral forests published before 1999 were re-identified using museum exhibits as *Pipistrellus pygmaeus* Leach, 1825 (Barlow & Jones, 1999; Kruskop, 2007).

In addition to our summer surveys, in 2016–2019 we determined the species composition of wintering bats in the northern and middle taiga subzones, and the microclimate conditions in the hibernacula. A total of 13 mine galleries and five underground fortifications were surveyed (Fig. 2). The census was done by visually examining the whole space for bats. Microclimate characteristics in the sites occupied by hibernating bats in underground winter roosts were measured by a handheld Testo 410-2 vane anemometer with humidity and temperature sensors (Germany). The temperature radiated from surfaces inside the shelter and the body surface temperature of bats (n = 90: nine individuals of *M. mystacinus*, 12 *M. brandtii*, 11 *Myotis daubentonii* Kuhl, 1817, ten *Plecotus auritus* Linnaeus, 1758, 48 *Eptesicus nilssonii* Keyserling & Blasius, 1839) were measured by Testo 875-1i thermal imager with Super Resolution option. The resultant electronic thermograms were treated with Testo IRSoft (ver. 4.0) software.

Results and Discussion

Analysis of the material in Table 1 reveals a regular increase in the bat species richness from north to south in the forest zone of European Russia. The same trend is observed also for the whole of Western Europe (Pereswiet-Soltan, 2007). Previously, only one to three species have been known from some PAs in the northern and middle taiga, where hardly any specialised bat

censuses were carried out. For a majority of the PAs (Paanajarvi NP, Kalevalsky NP, Vodlozersky NP, Kenozersky NP, and Kostomukshsky SNR), data on bats were missing altogether. The main source of information from SNR and NP of the Murmansk region, Arkhangelsk region and the Republic of Karelia has been accidental encounters. Only the application of ultrasound detection has recently enabled the collection of mass-scope information on the bat species composition in some PAs in North European Russia. We recorded the presence of bats on 447 occasions representing 447 bats at minimum. There were *Myotis nattereri* Kuhl, 1817*, M. brandtii/mystacinus, M. daubentonii, M. dasycneme* Boie, 1825*, Plecotus auritus, Nyctalus noctula* Schreber, 1774*, Eptesicus nilssonii, Vespertilio murinus* Linnaeus, 1758. Besides, 26 bat individuals belonging to four species were captured (*Myotis mystacinus, M. brandtii, M. daubentonii, Eptesicus nilssonii*).

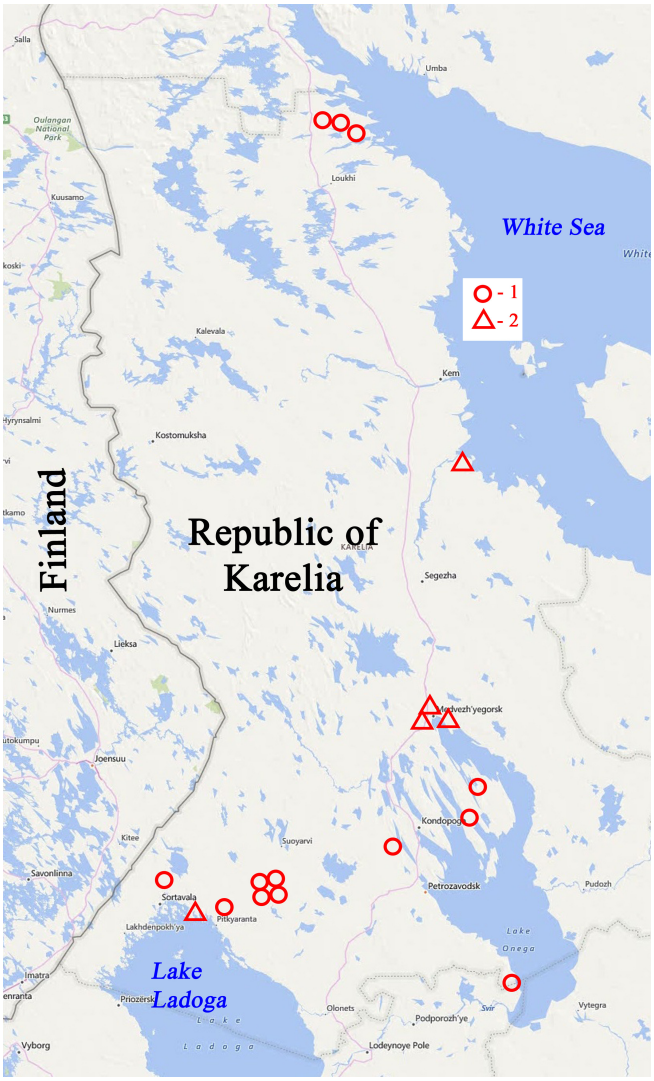

Fig. 2. Locations of underground hibernacula surveyed in the northern and middle taiga of the Republic of Karelia. Designations: 1 – mine galleries, 2 – fortifications.

Surveys in southern taiga forests, sub-boreal forests and nemoral forests in PAs yielded records of 8 to 12 species (Table 1). The main census method was mist-netting, which provides the most successful results. Importantly, this is a long-term effort, often arranged as monitoring.

The relative bat abundance in northern and middle taiga PAs features a dominance of *Eptesicus nilssonii* (Table 2). This is their major difference from PAs in more southern parts of the forest zone (Table 3), which are noted for the absence or scantiness of *E. nilssonii* and *Plecotus auritus*, a high share of *Nyctalus noctula* and *Pipistrellus nathusii* Keyserling & Blasius, 1839, and the presence of *Nyctalus leisleri* Kuhl, 1817 and *Pipistrellus pygmaeus*.

PAs above the Arctic Circle (Murmansk region) have yielded no records of species other than *E. nilssonii* for decades. Our several-days-long ultrasound detection surveys in the Polar-Alpine Botanical Garden Institute produced no encounters of this species either. There are no reports of its wintering in the Murmansk region. Consequently, at the northern limit of its distribution range, *E. nilssonii* is a Red Data Book species in the Murmansk Region (Boiko, 2014). The explanation is not only that the species encounters are not annually regular in the region, including its PAs (Pasvik SNR, Kandalakshsky SNR, Laplandsky SNR) (Semenov-Tjan-Shanskii, 1982; Boiko, 2014; Kataev, 2018), but also that there have been hardly any specialised bat censuses in the region and information about the species is clearly deficient. However, *E. nilssonii* may be subject to unexpected population changes. In Sweden (Rydell et al., 2020), decades-long monitoring of *E. nilssonii* on a 27-km long road revealed a sharp decline in the local population of this species, wherefore it is assumed that its conservation status may have been changed.

Our ultrasound detection surveys in the Paanajarvi NP were carried out late July 2018, and yielded records of four species (*Plecotus auritus, Nyctalus noctula*, *Eptesicus nilssonii* and *Vespertilio murinus*). They were encountered both in forest sites along the road running from the south to the north of the PA, and along the River Olanga in forest and farmland habitats. Paanajarvi NP and its northern surroundings (66.343243° N, 30.343737° E) are the northernmost points where *P. auritus, N. noctula*, and *V. murinus* have been recorded in the Northern Europe. This is much farther north than the

species ranges indicated in IUCN maps (www.iucnredlist.org). Interestingly, previous studies using a stable isotope approach predicted the origins of some *N. noctula* populations to be farther north than the current species range according to IUCN (Lehnert et al., 2014; Voigt et al., 2016). The only species recorded at Lake Paanajarvi itself was *N. noctula*. The Paanajarvi NP may also harbour *Myotis daubentonii* reported by Finnish researchers (Siivonen & Wermundsen, 2008) from the mouth of the River Oulankajoki into Lake Paanajarvi in Finland.

Table 1. Summer bat populations in Protected Areas (PAs) in the forest zone of European Russia

PA, region, № in Fig. 1	PA size, km^2	Species composition*	Survey method**	Source
Northern taiga				
Pasvik SNR, Murmansk region, №1	147.27	En	1	Kataev, 2018
Botanical Garden Institute, Murmansk region, №2	16.70	–	3	our data
Laplandsky SNR, Murmansk region, №3	2784.36	En	1	Semenov-Tjan-Shanskii, 1982
Kandalakshsky SNR, Murmansk region, №4	705.00	En	1	Boiko, 2014
Paanajarvi NP, Republic of Karelia, №5	1043.54	Pla, Nn, En, Vm	3	our data
Kalevalsky NP, Republic of Karelia, №6	744.00	Mdas, Pla, Nn, En	1,3	our data
Kostomuksha SNR, Republic of Karelia, №7	492.59	Mdb, Pla, Nn, En, Vm	1,3	our data
Pinega SNR, Arkhangelsk region, №8	518.90	Mbr, En, Vm	1,3	our data; Rykov, 2008a
Kozhozersky Landscape Sanctuary, Arkhangelsk region, №9	2016.05	En	1	Mamontov, 2006
Middle taiga				
Valaam Archipelago Nature Park, Republic of Karelia, №10	247.00	Mbr, Mdb, Pla, Nn, En, Vm	1,2,3	our data; Bogdarina, 2004
Vodlozersky NP, Republic of Karelia, №11	1306.00	Mn, Mbr, Mdb, Mdas, Pla, Nn, En, Vm	1,2,3	our data
Kivach SNR, Republic of Karelia, №12	108.70	Mm, Pla, En	1	our data; Zimin & Ivanter, 1969
Kenozersky NP, Arkhangelsk region, №13	1402.18	Mdb, Mdas, Pla, Nn, En	1,3	our data
Nizhne-Svirsky SNR, Leningrad region, №14	423.90	Mdb, Pla, En, Vm	1	Starikov & Popov, 2012
Southern taiga				
Darwin SNR, Vologda region and Yaroslavl regions, №15	1127.00	Mbr, Mdb, Mdas, Nl, Nn, Pn, En, Vm	2	Vasenkov & Sidorchuk, 2010
Sub-boreal forests				
Smolenskoye Poozerye NP, Smolensk region. №16	1462.37	Mm, Mbr, Mdb, Pla, Nl, Nn, Ppyg, Pn, En, Vm	2	Vasenkov et al., 2017
Oksky SNR, Ryazan region, №17	560.27	Mm, Mbr, Mdb, Mdas, Pla, Nl, Nn, Ppyg, Pn, En, Vm	2	Vlaschenko et al., 2016
Prioksko-Terrasny SNR, Moscow region, №18	49.45	Mn, Mbr, Mdb, Mdas, Pla, Nl, Nn, Ppyg, Pn, Vm	1,2,3	Albov et al., 2009
Nemoral forests				
Bryansky Les SNR, Bryansk region, №19	121.86	Mbr, Mdb, Pla, Nl, Nn, Nlas, Ppyg, Pn, Pk, En, Es, Vm	1,2,3	Vlaschenko et al., 2016; Sitnikova et al., 2009; Shpilenok et al., 1997
Mordovia SNR, Republic of Mordovia, №20	321.62	Mn, Mbr, Mdb, Mdas, Pla, Nn, Ppyg, Pn, Pk	1,2,3	Artaev & Smirnov, 2016
Smolny NP, Republic of Mordovia, №21	365.00	Mbr, Mdb, Mdas, Pla, Nn, Ppyg, Pn, Pk	1,2,3	Artaev & Smirnov, 2016

Note: * Designations: Mn – *Myotis nattereri,* Mm – *M. mystacinus*, Mbr – *M. brandtii*, Mdb – *M. daubentonii*, Mdas – *M. dasycneme*, Pla – *Plecotus auritus,* Nl – *Nyctalus leisleri*, Nn – *N. noctula*, Nlas – *N. lasiopterus* Kuhl, 1817, Ppyg – *Pipistrellus pygmaeus*, Pn – *P. nathusii*, Pk – *P. kuhlii* Kuhl, 1817, En – *Eptesicus nilssonii*, Es – *E. serotinus* Schreber, 1774, Vm – *Vespertilio murinus*; ** Survey method: 1 – visual observations and sampling of biological material, 2 – mist-netting, 3 – ultrasound detection.

Table 2. Relative abundance (%) of bats in PAs in the northern and middle taiga subzone of European Russia (our data, ultrasound detection)

Species	Kalevalsky NP	Kostomuksha SNR	Valaam Archipelago Natural Park	Vodlozersky NP	Kenozersky NP
Myotis nattereri	–	–	–	1.3	–
Myotis brandtii/mystacinus	–	–	–	5.1	–
Myotis daubentonii	–	5.3	1.0	9.0	12.0
Myotis dasycneme	2.6		2.0	11.5	4.0
Plecotus auritus	2.6	5.3	5.9	24.4	12.0
Nyctalus noctula	46.1	5.3	44.1	9.0	16.0
Eptesicus nilssonii	48.7	73.6	41.4	33.3	56.0
Vespertilio murinus	–	10.5	5.9	6.4	–

Table 3. Relative abundance (%) of bats in PAs in the southern taiga subzone, sub-boreal forests and nemoral forests of European Russia (according to Albov et al., 2009; Vasenkov & Sidorchuk, 2010; Vlaschenko et al., 2016; Vasenkov et al., 2017; method: mist-netting)

Species	Darwin SNR	Smolenskoye Poozerye NP	Oksky SNR	Prioksko-Terrasny SNR	Bryansky Les SNR
Myotis nattereri	–	–	–	3.5	–
Myotis mystacinus	–	0.2	0.3	–	–
Myotis brandtii	1.1	0.8	7.3	13.2	12.2
Myotis daubentonii	37.8	2.3	17.0	14.0	3.9
Myotis dasycneme	14.6	–	6.2	9.6	–
Plecotus auritus	–	0.8	4.1	0.9	1.9
Nyctalus leisleri	–	2.3	4.1	1.8	1.9
Nyctalus noctula	13.6	38.7	35.8	5.3	41.2
Pipistrellus pygmaeus	–	1.2	2.9	6.1	6.5
Pipistrellus nathusii	19.4	22.6	17.3	43.8	21.9
Eptesicus nilssonii	2.4	0.4	–	–	–
Vespertilio murinus	11.2	30.7	5.0	1.8	10.3

According to Strelkov (1997a,b), the limit of the breeding range in Northwest Russia lies at 60° N for *Nyctalus noctula*, and even slightly farther north for *Vespertilio murinus*. We speculate that the distribution range of these migratory species might extend even farther north owing to barren and immature animals, as corroborated by the results of our acoustic surveys in the middle and even northern taiga subzones, as well as by data from the latest Atlas of Finnish Bats (Tidenberg et al., 2019).

Presumably, the range expansion of migratory bat species has, in part, been promoted by the change of some climate parameters in the region. For instance, in the Kivach SNR (62.276513° N, 33.981624° E), the change since 1970 has been a 1.4°C rise in average of the annual air temperature, a 23-day increase in climatic summer duration, and 52 more frost-free days on soil surface (Skorokhodova & Shcherbakov, 2011). Such changes might alter the seasonal bat migrations along the latitudinal gradient.

In 2019, our surveys in the Kalevalsky NP produced records of four species (*Myotis dasycneme, Plecotus auritus, Nyctalus noctula,* and *Eptesicus nilssonii*). A major part of the Kalevalsky NP could not be surveyed because of the near absence of drivable roads. Therefore, only the eastern part of the PA was studied. In the censuses, *Eptesicus nilssonii* dominated (48.7%), and it was recorded from Sudnozero, an only inhabited village in the Kalevalsky NP. It was on the shore of the lake bearing the same name, along the road from Sudnozero village to Pongaguba village. Two *E. nilssonii* individuals were sighted on a forest lakelet 70 m in diameter. *Plecotus auritus* records come from the road to the Sudnozero village, and from the immediate vicinities of the Kalevalsky NP, to the south, north and east of the PA. The relative abundance of this species was 2.6%. *Nyctalus noctula* was noted in the Kalevalsky NP on the River Sudno, on Lake Sudnozero, and along the road to the village Sudnozero. The sequences of signals implying unique species identification were 17–297 pulses. It was twice sighted over the water, along the shoreline. In contrary to our expectations, the species' relative abundance was very high (46.1%). *Myotis dasycneme* was recorded on Lake Sudnozero. In the nearest vicinity of the Kalevalsky NP, the species occurred along the shoreline of some nameless lakes to the south and east of the border of this PA. Its relative abundance was 2.6%. *Myotis dasycneme* records from the Kalevalsky NP and its surroundings represent the northernmost locations detected for the species (65.029154° N, 30.364445° E) by ultrasound detection monitoring of bats in North European Russia.

In the Kostomuksha SNR (Fig. 3), our surveys in 2018 revealed five bat species (*Myotis daubentonii, Plecotus auritus, Nyctalus noctula, Eptesicus nilssonii,* and *Vespertilio murinus*). We also detected *P. auritus* and *V. murinus* in the buildings of the Kostomuksha SNR's Visitor Centre (0.17 km^2 of forest with a lake and a small river) in the Kostomuksha settlement. *Eptesicus nilssonii* dominates in the Kostomuksha SNR in terms of relative abundance (73.6%). This was the only species recorded in two 40-km transects. Its relative density was 0.075 individuals per 1 km of transect. *Nyctalus noctula* was encountered along the water transect on Lake Minozero, *Myotis daubentonii* at a fixed point on the River Kamennaya, and *V. murinus* on a forest lakelet near Lake Kalevi.

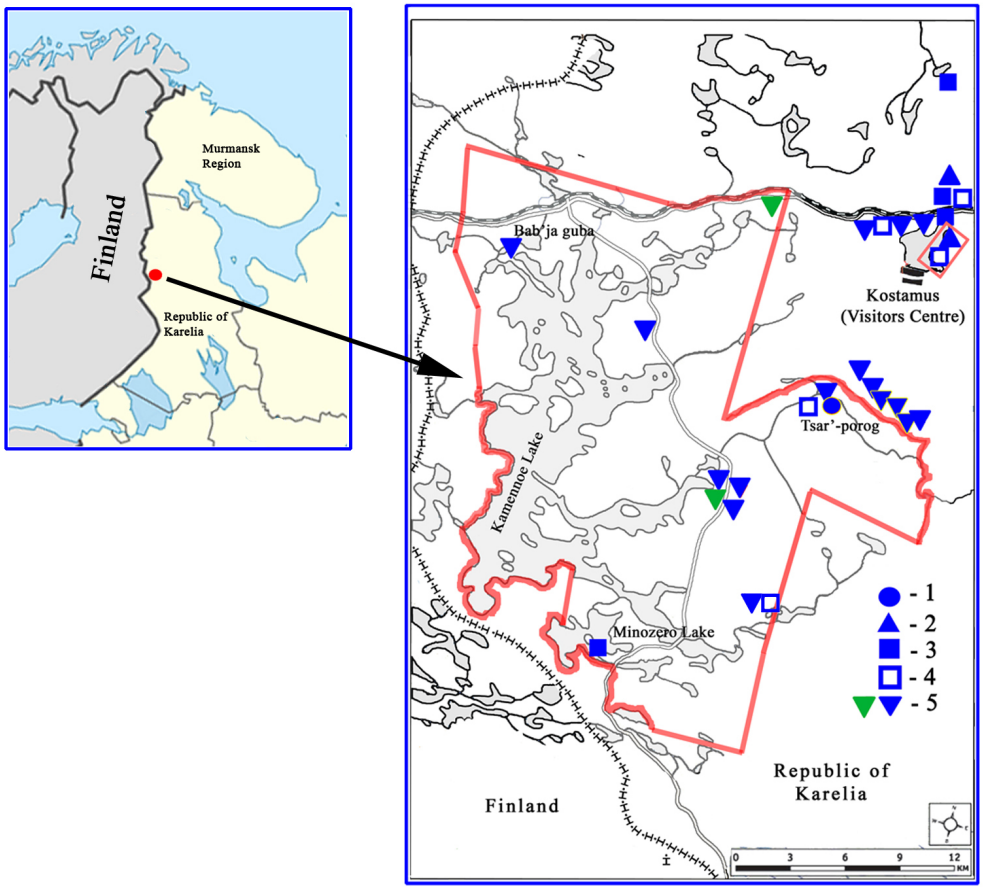

Fig. 3. Locations of bat records in the Kostomuksha State Nature Reserve. Designations: 1 – *Myotis daubentonii*, 2 – *Plecotus auritus*, 3 – *Nyctalus noctula*, 4 – *Vespertilio murinus*, 5 – *Eptesicus nilssonii* (green symbol – visual observations, blue symbols – ultrasound detections).

The results of censuses in the Metsola Biosphere Reserve (BR), which has an international status and incorporates areas of the Kalevalsky NP, Kostomuksha SNR and the Kostomuksha municipality, are given collectively for its component parts. In the Metsola BR, the bat species composition includes seven species (*Myotis nattereri*, *M. daubentonii, M. dasycneme, Plecotus auritus, Nyctalus noctula, Eptesicus nilssonii, Vespertilio murinus*), of which four (excluding *M. daubentonii* and *M. dasycneme*) were recorded in the Kostomuksha settlement and its green belt. Here, like in the Kalevalsky NP, the sequences of pulses uniquely identified as belonging to *N. noctula* were unusually long (23–346 pulses). Records from water transects and fixed points include Lake Lamasjarvi (*P. auritus, E. nilssonii, V. murinus*), Lake Sudnozero (*M. dasycneme, N. noctula, E. nilssonii*), Lake Kamennoye (*E. nilssonii*), Lake Minozero (*N. noctula*), Lake Koriangi (*N. noctula*), forest lakelets (*M. dasycneme, P. auritus, N. noctula, E. nilssonii*), River Kamennaya (*M. daubentonii, E. nilssonii, V. murinus*), River Sudno (*N. noctula*), River Tollojoki (*M. daubentonii*), River Kyurelya (*M. dasycneme, N. noctula*), River Selvana (*M. nattereri, M. daubentonii, M. dasycneme, N. noctula*), River Livo (*P. auritus*), and River Zhiga (*N. noctula*).

The above mentioned species, except perhaps for *M. nattereri* and *M. dasycneme*, are widespread in the Metsola BR, and occur both in forest habitats and in water bodies. Recording of *M. nattereri* from an area reaching beyond PAs is quite explicable. Similar results have been reported before for other PAs (Mordovia SNR and Smolny NP) and the administrative units in which they are situated in the nemoral forest zone (Artaev & Smirnov, 2016). The total relative density of chiropterans in the Metsola BR based on surveys of seven 40-km transects was 0.289 individuals per km, including *M. dasycneme* with 0.007 individuals per km, *P. auritus* with 0.021 individuals per km, *N. noctula* with 0.143 individuals per km, *E. nilssonii* with 0.100 individuals per km, and *V. murinus* with 0.018 individuals per km.

Summer car surveys with ultrasound detection along Pinega SNR outer borders in 2017, along a 40-km transect from the village Pinega to the southern end of the Pinega SNR, detected

18 *E. nilssonii* individuals and two *V. murinus* individuals. *Vespertilio murinus* was spotted on a lakelet where the road from Krasnaya Gorka forks to Maletino and to the village Pershkovo. *Eptesicus nilssonii* records come from the village Pinega, lakelets outside of this village, Krasnaya Gorka – Maletino road fork, Pekhorovsky creek, rivers Karjela and Belaya, as well as other points along the road to the southern end of the SNR. The relative density of *E. nilssonii* was 0.450 individuals per km of transect, the one of *V. murinus* (0.050 individuals per km), and is in total 0.500 individuals per km transect. Chiropteran censuses in karst caves near the Pinega SNR revealed the overwintering of two bat species (*M. brandtii* and *E. nilssonii*) (Rykov, 2008a,b). *Eptesicus nilssonii* predominated there. It is quite safe to say that all these species are present inside the Pinega SNR, too.

Chiropteran censuses in the Valaam Archipelago Natural Park (Lake Ladoga) in 2016 demonstrated the highest relative abundance for *N. noctula*, which could be expected, given the suitable climate and environmental conditions (Kravchenko & Lazareva, 1989; Verzilin et al., 1990). There being few roads and plenty of important sights of interest, surveys were done both by car and on foot, taking stops at fixed points. Bat records on Valaam Island are schematically mapped in Fig. 4.

Records from separate study sites of Valaam Island included: Valaam Archipelago Natural Park's office area (*Plecotus auritus*, *Nyctalus noctula*, *Eptesicus nilssonii*, *Vespertilio murinus*), winter hotel, orchard (*N. noctula*, *E. nilssonii*), Preobrazhenskiy Cathedral (*E. nilssonii*, *V. murinus*), outskirts of fields behind the cathedral (*N. noctula*, *E. nilssonii*), monastery bay (*P. auritus*, *N. noctula*, *E. nilssonii*), larch alley, Hegumen's cemetery (*N. noctula*, *E. nilssonii, V. murinus*), helicopter landing site, farmland (*N. noctula*), Kukinsky Bay (bridge) (*N. noctula*), Tikhvinsky bridge (*N. noctula*, *E. nilssonii*), Lake Leshchyovoye (*N. noctula*, *E. nilssonii*), Old quay (Lake Ladoga) (*E. nilssonii*), 20-year-old pine forest (*P. auritus*, *N. noctula*), Vladimirsky bridge (*Myotis daubentonii, M. dasycneme*, *E. nilssonii*), White skete (*E. nilssonii*), first bridge to the skete of St. Nicholas (*M. dasycneme*, *N. noctula*, *E. nilssonii*), second and third bridges (*E. nilssonii*, *V. murinus*), chapel along the road to Kazansky skete (*P. auritus*, *N. noctula*, *E. nilssonii*), Kazansky skete (*N. noctula*, *E. nilssonii*). Previously, Bogdarina (2004) captured *M. daubentonii, P. auritus* and *E. nilssonii* in mist nets (Fig. 4, red symbols).

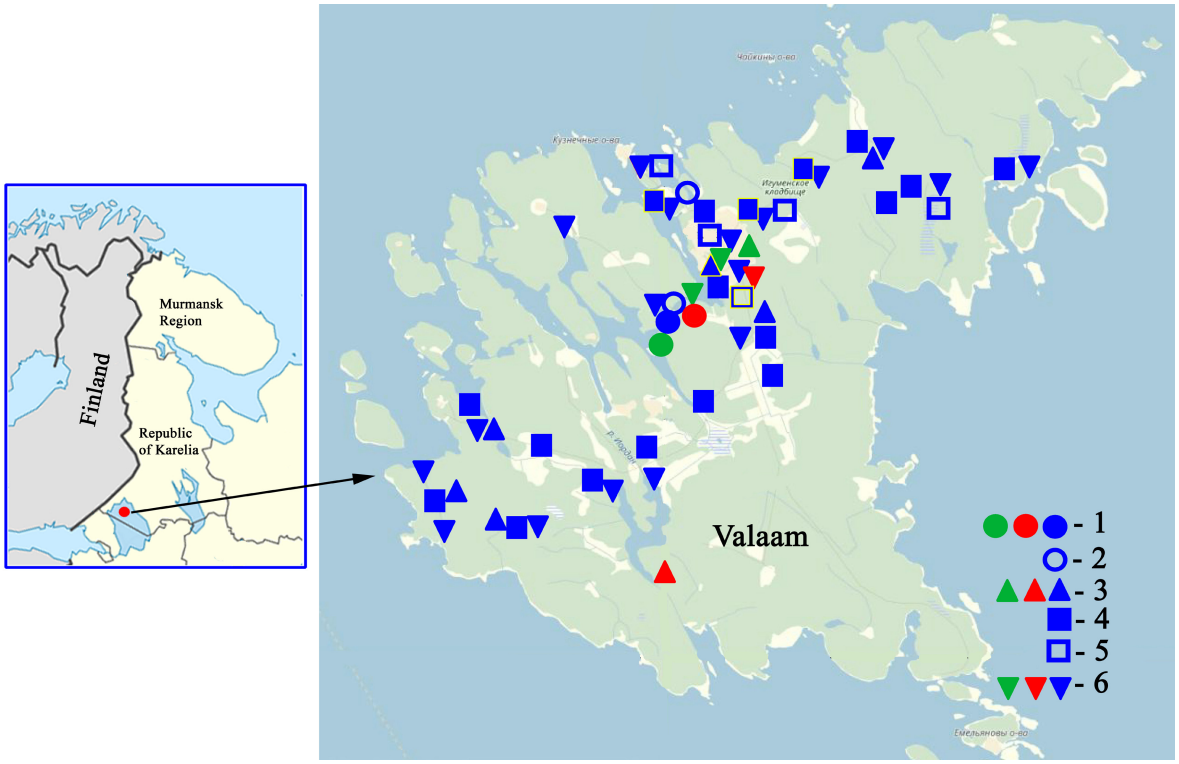

Fig. 4. Bat records in Valaam Archipelago Natural Park. Designations: 1 – *Myotis daubentonii*, 2 – *Myotis dasycneme*, 3 – *Plecotus auritus*, 4 – *Nyctalus noctula*, 5 – *Vespertilio murinus*, 6 – *Eptesicus nilssonii* (green symbols – visual observations and sampling of biomaterial, red – mist-netting, blue – ultrasound detections).

No specialised bat surveys have been carried out in the Kivach SNR. *Plecotus auritus* and *E. nilssonii* were encountered in its area in the mid-XX century (Zimin & Ivanter, 1969). There had been no further accessions to this short list for many years until a recent finding of *Myotis mystacinus* (two dead animals in Kivach village). It is also worth mentioning that *M. mystacinus, M. brandtii, M. daubentonii*, and *E. nilssonii* have been encountered in different years during winter surveys in mine galleries in Pertnavolok (9 km from the southern border of the Protected Area). One can expect all these species to occur inside the Kivach SNR, too.

In 2019, Vodlozersky NP was surveyed using mist-netting (Pilmasozero, Sukhaya Vodla, Okhta, Vama, Kukshezero and Navdruchey), as well as by ultrasound detection at fixed points and along car transects (Table 4, Fig. 5). Additionally, two *Myotis brandtii* were captured at daytime roosts in an abandoned old house at Pilmasozero post and two more unidentified bats were sighted in the firewood shed at the Sukhaya Vodla post.

Ultrasound detection at fixed points revealed a wider bat species composition than mist-netting. We also found a high relative abundance of *Myotis daubentonii* and *M. dasycneme*, occurring on the water bodies which shores were surveyed.

In Vodlozersky NP, this combination of methods produced data on the dominance or high relative abundance of *Eptesicus nilssonii* (Table 4), but it was less pronounced than in the middle taiga subzone on average (Belkin et al., 2018). Only *E. nilssonii* was encountered in the standard 40-km transect, yielding a relative density of 0.150 individuals per km of transect. The species has been repeatedly encountered in winter roosts outside living buildings in the village Kuganavolok and at the Vama post. Noteworthy are the unusually frequent encounters of *Plecotus auritus* in a stretch of the road Kuganavolok – River Navdruchey. Possibly, this area offers *P. auritus* the best conditions for daytime roosting and nighttime activity.

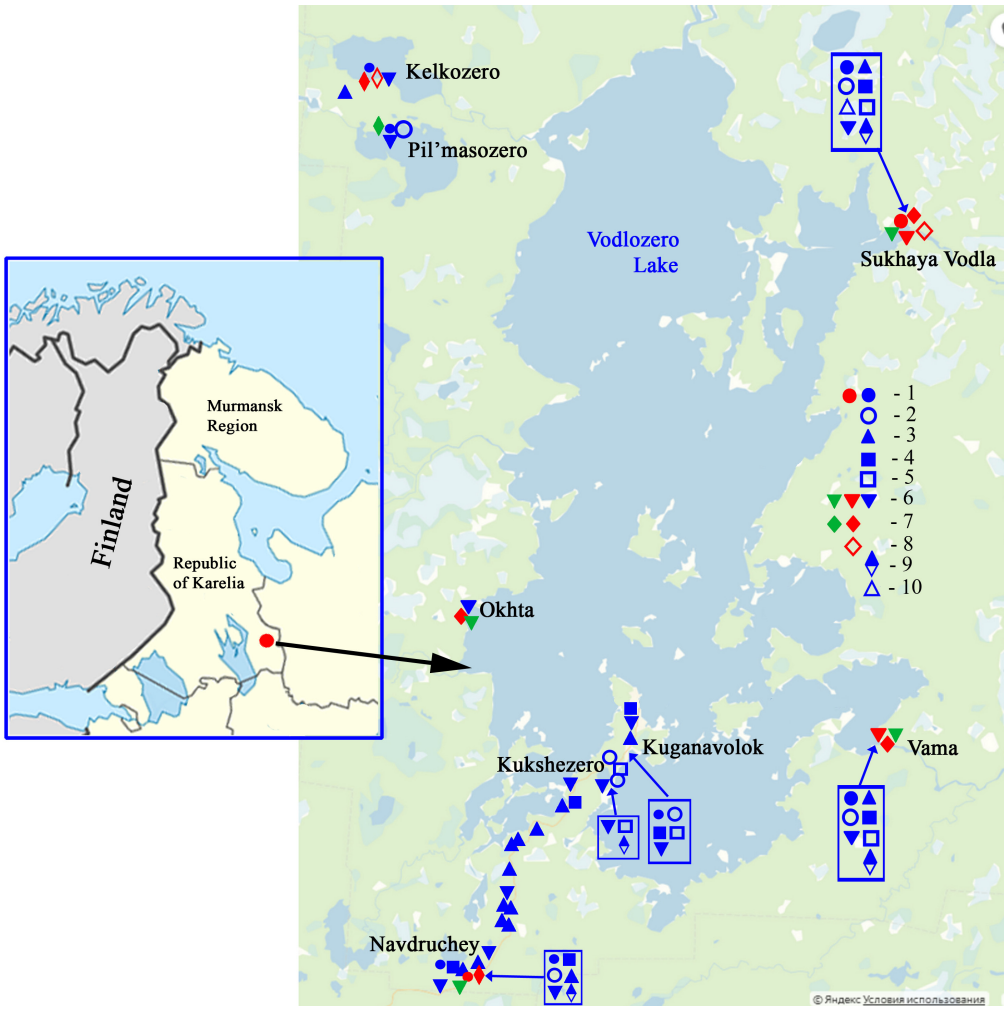

Fig. 5. Bat records in the Vodlozersky National Park. Designations: 1 – *Myotis daubentonii*, 2 – *Myotis dasycneme*, 3 – *Plecotus auritus*, 4 – *Nyctalus noctula*, 5 – *Vespertilio murinus*, 6 – *Eptesicus nilssonii*, 7 – *Myotis brandtii*, 8 – *Myotis mystacinus*, 9 – *Myotis brandtii/mystacinus*, 10 – *Myotis nattereri* (green symbols – visual observations and sampling of biomaterial, red – mist-netting, blue – ultrasound detections).

Table 4. Relative abundance (%) of bats in the Vodlozersky National Park

Species	Mist-netting	Ultrasound detection		
		At fixed points	Along car transects	Total
Myotis nattereri	–	2.6	–	1.3
Myotis mystacinus	10.7	–	–	–
Myotis brandtii	46.4	–	–	–
Myotis brandtii/mystacinus	–	10.3	–	5.1
Myotis daubentonii	7.2	18.9	–	9.0
Myotis dasycneme	–	15.3	7.7	11.5
Plecotus auritus	–	10.3	38.4	24.4
Nyctalus noctula	–	10.3	7.7	9.0
Eptesicus nilssonii	35.7	23.0	43.6	33.3
Vespertilio murinus	–	10.3	2.6	6.4

At some points in the surveys, the results of mist-netting and ultrasound detection of bats suggest that the Sukhaya Vodla post had a colony of *Eptesicus nilssonii*, while the Vama post had a colony of *Myotis brandtii*. Summer findings of *Myotis mystacinus* at the Sukhaya Vodla post and Lake Kelkozero (62.224867° N, 37.081629° E and 62.466342° N, 36.673240° E) are the northernmost records in European Russia.

In 2017, bat censuses by ultrasound detection in Kenozersky NP revealed five bat species (*Myotis daubentonii, M. dasycneme*, *Plecotus auritus*, *Nyctalus noctula*, and *Eptesicus nilssonii*) along car transects and water transects, as well as at fixed points. Besides, *Vespertilio murinus* was recorded from the village Afanasovskaya (30 km east of the Kenozersky NP border). The prevalent species in the Kenozersky NP was *E. nilssonii*; its relative abundance was 56%, while other species contributed 4% to 16% (Table 2). Surveys of four standard 40-km transects showed the overall relative density of bats in Kenozersky NP to be 0.115 individuals per km of transect, and like in the majority of other PAs, *E. nilssonii* was the dominant species (Table 5).

The above mentioned results demonstrated that *Eptesicus nilssonii* dominates in bat communities in the middle and northern taiga. The calculated relative densities of *E. nilssonii* in Karelia along the north-to-south gradient reached a maximum of 0.708 individuals per km of transect at 64–65° N. The values of this parameter decline both to the south and to the north of this belt, with a minimum of 0.125 individuals per km above 66° N. *Eptesicus nilssonii* encounters can be expected to get rarer and more fragmentary from the Arctic Circle to the northern limit of the forest zone, as it is observed in Finland (Mitchell-Jones et al., 1999; Tidenberg et al., 2019), in correlation with forest vegetation characteristics, altitudinal gradient, minimum air temperatures during breeding and hibernation (Michaelsen, 2016). As it was demonstrated by long-term observations in a place in Sweden, the decline in number of *E. nilssonii* was not only latitudinally, but also over time (Rydell et al., 2020). On the other hand, this species benefits from some ecological (hibernating in underground spaces of varying structure and microclimate, open or single localisation inside the hibernacula, later occupation of hibernacula in autumn and earlier emergence from hibernation compared to other species), physiological and biochemical advantages. They enable it to dominate in the northern and middle taiga subzones in terms of relative densities and relative abundances in winter and summer, as well as prevalence in human settlements and at water bodies in summer and in underground hibernacula in winter (Belkin et al., 2019a,b,c). *Eptesicus nilssonii* demonstrated a high ecological valence, including tolerance of extremely low temperatures at hibernacula (Fig. 6). Our studies showed *E. nilssonii* to be more tolerant than other species towards temperature, but not towards air humidity. As a result, *E. nilssonii* can live and breed up to a latitude of 70° N (Rydell et al., 1994).

Table 5. Relative density (individuals per km of transect) and locations of bats in Kenozersky National Park

Species	Relative density	Locations
Myotis daubentonii	–	Lakes Lekshmozero, Kenozero, Svinoye
Myotis dasycneme	0.005	Lake Svinoye
Plecotus auritus	0.010	Gory village, Sudorskaya Lahta Bay of Lake Kenozero, forest road to the north of Lake Kenozero
Nyctalus noctula	0.025	Morshchihinskaya and Vershinino villages, watershed, Sudorskaya Lahta Bay of Lake Kenozero
Eptesicus nilssonii	0.075	Villages (Morshchihinskaya, Orlovo, Maselga, Vershinino, Pershlahta, Filippovskaya, Ust-Pocha), rivers (Sondola, Khabyanzya), Sudorskaya Lahta Bay of Lake Kenozero

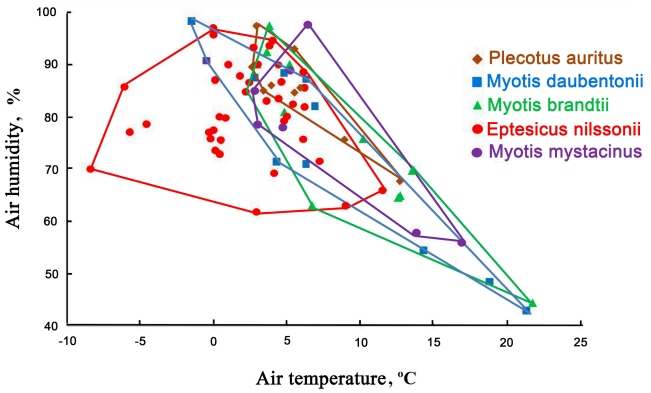

Fig. 6. Air temperature and humidity parameters typical for different bat species in underground hibernacula in the northern and middle taiga subzones. Each point represents the air temperature and humidity at the position where the bat individuals were found in underground hibernacula.

In general, PAs have an important role in the conservation of bat habitats in regions with extensive logging. They act as refugia where human pressure on chiropterans is minimised. Another specific characteristic of forest in PAs is the ample presence of dead standing trees. The availability of such trees, which usually have hollows and loose bark on trunks, can be an important factor for forest-dwelling bat species choosing daytime roosts and locations for the colony in summer (Ilyin et al., 2003; Dietz & Kiefer, 2016), and for hibernation in winter. Thus, according to archival data from the Kalevalsky NP, where old-growth pine (*Pinus sylvestris* L.) forests prevail, there were 800–2000 hollowed trees per km^2. In the Vodlozersky NP, where primary spruce (*Picea abies* (L.) Karst.) forests occupy 50.2% of the Vodlozersky NP's forest-covered area and the contribution of *Pinus sylvestris* L., *Betula* sp. and *Populus tremula* L. is substantial (up to 30%), there were 2600–7600 dead standing trees per km^2 (Ananev et al., 2001). Middle taiga pine forests aged 120–140 years contain 16 000 dead standing trunks per km^2 (Moshnikov et al., 2019). Their average diameter is 24 cm. Our own previous counts of *P. tremula* thicker than 20 cm in diameter, in which hollows occur the most frequently, showed that the number of such trees in various forest types in the middle taiga subzone varied at 200–2200 trees per 1 km^2 (Belkin et al., 2012). In native spruce stands, thick *P. tremula* are usually distributed more or less evenly, growing in small groups (2–4 trees). In mature secondary spruce stands, *P. tremula* usually grow in groups of 5–10 trees or in patches occupying up to 0.005 km^2 (Volkov, 2008). Much attention is given to retention of dead standing and hollow-bearing trees in restricted areas during forest management and mitigation of forestry impact on bats (Law et al., 2016), irrespective of the forest type or geographical region.

In the conservation of bats, a special role belongs to Red Data Books, which urge specialists and the general public to focus more specifically on the most threatened species. Yet, the species checklists in some regional Red Data Books (Table 6) need to be revised, since they have grown outdated and new lists are being prepared in the meantime. For instance, in the Republic of Karelia, the revision will be done in 2020, supposedly leaving only two species on the Red Data Book list (*Myotis mystacinus* and *Plecotus auritus*), who live at the northern limit of their distribution ranges and have the lowest relative abundances at hibernacula (Belkin et al., 2018). The Red Data Book of the Murmansk region will retain *E. nilssonii*. The plan for the Red Data Book of the Arkhangelsk region is to keep *Myotis dasycneme, M. brandtii, Plecotus auritus* as the least studied species. In the southern taiga subzone, such revisions have already been made in the Leningrad region and are upcoming in the Vologda region.

Table 6. The bat species of the regional Red Data Books in the taiga zone of European Russia

Region	*Myotis nattereri*	*Myotis mystacinus*	*Myotis brandtii*	*Myotis daubentonii*	*Myotis dasycneme*	*Plecotus auritus*	*Nyctalus leisleri*	*Nyctalus noctula*	*Eptesicus nilssonii*	*Vespertilio murinus*	Authors
Murmansk region	–	–	–	–	–	–	–	–	+	–	Boiko, 2014
Republic of Karelia	–	+	–	+	+	+	–	–	–	–	Korosov, 2007
Arkhangelsk region	–	–	+	–	–	+	–	–	–	–	Rykov, 2008 b
Leningrad region	+	+	+	–	+	–	–	–	–	–	Chistyakov, 2018
Vologda region	–	+	–	+	+	+	+	+	–	+	Konovalov, 2010

Conclusions

Data reported above demonstrated that in PAs of the forest zone in European Russia, the bat populations are diverse. Their species richness increases in southward direction. *Eptesicus nilssonii* dominates in bat communities in the northern and middle taiga subzones. By the northern limit of its geographical range it turns into the only representative of the bat fauna. On the other hand, *E. nilssonii* is absent from more southern parts of the forest zone, or its relative abundance there is minimal, while the dominant faunal elements are *Myotis daubentonii* (Darwin SNR), *N. noctula* (Smolenskoye Poozerye NP, Oksky SNR and Bryansky Les SNR) and *Pipistrellus nathusii* (Prioksko-Terrasny SNR).

In contrary to our previous assumptions, *Nyctalus noctula* and *Vespertilio murinus* have been regularly recorded by ultrasound detection in both northern and middle taiga, which is a new finding. Their northernmost records alongside *Plecotus auritus* and *Eptesicus nilssonii* come from 66.343243° N, 30.343737° E, and alongside *Myotis dasycneme* from 65.029154° N, 30.364445° E. Vodlozersky NP yielded the northernmost records of *Myotis mystacinus* in European Russia (62.224867° N, 37.081629° E and 62.466342° N, 36.673240° E), and its co-encounters together with *Myotis brandtii*, i.e. at hibernacula, suggest these species are sympatric, like they are in other parts of the species ranges. In general, PAs act as key refugia with minimal human pressure on bats, enhancing the overall well-being of chiropteran communities throughout the forest zone of European Russia.

Acknowledgements

The authors are grateful to E.A. Khizhkin and A.N. Lyapunov, as well as to the staff of the Protected Areas Yu.A. Krasovsky (Kostomuksha State Nature Reserve), E.V. Kholodov, E.N. Kholodova, V.N. Mamontov (Vodlozersky National Park), and S.I. Drovnina (Kenozersky National Park) for helping with the research. The study was carried out under state orders №0218-2019-0080 and №0218-2019-0073, RAS Presidium Programme №41 (project №0221-2018-0002), and with financial support from Kostomuksha State Nature Reserve, Vodlozersky National Park, and Kenozersky National Park.

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ОСОБЕННОСТИ НАСЕЛЕНИЯ ЛЕТУЧИХ МЫШЕЙ (CHIROPTERA) НА ОСОБО ОХРАНЯЕМЫХ ПРИРОДНЫХ ТЕРРИТОРИЯХ В ПОДЗОНАХ СЕВЕРНОЙ И СРЕДНЕЙ ТАЙГИ ЕВРОПЕЙСКОЙ РОССИИ

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Фауна летучих мышей (Chiroptera) особо охраняемых природных территорий (ООПТ) лесной зоны Европейской России в целом не оценивалась, хотя работы по отдельным ООПТ выходят достаточно регулярно. Вдоль широтного градиента эта обширная территория охватывает самые различные места обитания рукокрылых, пригодные для принципиально разнообразного состава населения летучих мышей. Для обзора видов летучих мышей мы сфокусировались на восьми ООПТ подзон северной и средней тайги, а также на кратком сравнительном обзоре фаунистической литературы в целом по лесной зоне Европейской России. По результатам учетов с использованием Bat-детектора и паутинных сетей, выявлены видовой состав, относительное обилие, относительная численность и распределение рукокрылых на ООПТ. Зарегистрировано девять видов летучих мышей: *Myotis nattereri*, *M. mystacinus, M. brandtii, M. daubentonii, M. dasycneme, Plecotus auritus, Nyctalus noctula, Eptesicus nilssonii, Vespertilio murinus*. Показана регулярная регистрация ультразвуковых сигналов *Plecotus auritus*, *Nyctalus noctula* и *Vespertilio murinus* до 66° N, что значительно севернее видовых ареалов, показанных на картах МСОП (IUCN Red List). При отсутствии специальных учетов в Карелии и Архангельской области на протяжении десятилетий этот результат стал неожиданным. Выявлено доминирование *Eptesicus nilssonii* в сообществах рукокрылых на ООПТ, что характерно только для подзон северной и средней тайги. Обсуждаются некоторые экологические предпочтения этого вида, такие как большая толерантность *E. nilssonii* по сравнению с другими видами в отношении температуры, но не влажности воздуха в зимних убежищах, позволяющие ему осваивать высокие широты. В то же время, в более южных частях лесной зоны *E. nilssonii* отсутствует или его относительное обилие минимально, а доминирующими видами выступают *Myotis daubentonii* (Дарвинский заповедник), *Nyctalus noctula* (национальный парк «Смоленское поозерье», Окский заповедник и заповедник «Брянский лес») и *Pipistrellus nathusii* (Приокско-Террасный заповедник). Результаты отлова рукокрылых паутинными сетями в национальном парке «Водлозерский» выявили самые северные точки встреч *Myotis mystacinus* на севере Европейской России (62.224867° N, 37.081629° E и 62.466342° N, 36.673240° E). В заключении, на основании последних учетов летучих мышей, мы обсуждаем необходимость пересмотра статуса рукокрылых в региональных Красных книгах.

Ключевые слова: видовой состав, Красная книга, относительное обилие, относительная численность, распространение